3

# Letter of Application

AND

# PRÉCIS OF CONTRIBUTIONS TO PHYSIOLOGY

OF


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Candidate for the Waynflete Professorship of Physiology
in the University of Oxford




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Ch. S. Sherrington
from A. D. Waller.

*Weston Lodge:*
**16** ***Grove End Road, London, N.W.***
*February 23rd,* 1895.

*My Lord Bishop and Gentlemen,—*

*I have the honour to present myself as a candidate for the Waynflete Chair of Physiology in the University of Oxford.*

*I am thirty-eight years of age. Since the date of my graduation at the University of Aberdeen* (1878) *I have been uninterruptedly engaged in the study and teaching of Physiology. During the last ten years I have held the appointment of Lecturer on Physiology to the St. Mary's Hospital Medical School, London, and in that capacity it has been my duty to organise a physiological and histological laboratory in accordance with the resources and requirements of a medical school. During the last year I have enlarged my own laboratory in order to supplement my ordinary teaching by lectures and demonstrations of a more original character. In support of my present application, I beg to submit to your consideration a résumé of my published work during the last fifteen years, and I venture further to submit as evidence of its value in the eyes of competent judges* (1) *that upon two occasions it has been favourably distinguished—by the Académie des Sciences, Paris; and by the Accademia delle Scienze, Bologna;* (2) *that it has found currency and acceptance in a book on Physiology, adopted as a text-book by many students and teachers of that science.*

*It has long been my desire to fittingly occupy a professorial chair; the tenor of my studies, both as a learner and as a teacher, has been directed to that end, and I have throughout acted on the belief that teaching and learning are mutually complementary. Enlarged opportunities and responsibilities such as attach to the Waynflete Professorship constitute the life-task with which I most desire to be entrusted.*

*I am,*

*My Lord Bishop and Gentlemen,*

*Your obedient servant,*

*AUGUSTUS D. WALLER.*

*To the Electors to the Waynflete Professorship of Physiology,*
*University of Oxford.*

## *CURRICULUM VITÆ*

| | | | Published Papers |
|---|---|---|---|
| Date of birth . . . . . . | 1856 | | |
| Commenced study of Medicine at the University of Aberdeen . . . | 1874 | *Class Prizes*: 1st in Physiology.<br>2nd in Histology.<br>2nd in Natural History.<br>1st in Clinical Medicine. | |
| Graduated M.B. . . . . . . | 1878 | | |
| Studied Medicine at the University of Edinburgh, and Physiology in the Leipzig Institute under Professor Ludwig . . . . . . | 1878–80 | . . . . . . . . | I. II. III. IV. |
| Graduated M.D. . . . . . . | 1881 | . . . . . . . . | VI. |
| "In medical practice" in London; studied Physiology at University College and at Lyons . . . . | 1881–2 | . . . . . . . . | V. VII. VIII. IX. |
| Appointed Lecturer on Physiology to the London School of Medicine for Women . . . . . . . | 1883 | | |
| Appointed Lecturer on Physiology to the St. Mary's Hospital Medical School, London . . . . | 1884 | | |
| | 1885–6 | . . . . . . . . . . | X. |
| | 1887 | "Mention honorable" de l'Académie des Sciences (conjointly with Professor E. W. Reid). | XI. XIII. |
| | 1888 | . . . . . . . . . . | XII. |
| | 1889 | Prix Montyon de Physiologie expérimentale, Académie des Sciences. | XIV. |
| | 1890 | . . . . . . . . . . | XV. XVI. |
| Published "An Introduction to Human Physiology" . . . . . . | 1891 | . . . . . . . . | XVII. XVIII. XX. XXI. XXII. |
| | 1892 | Premio Aldini sul Galvanismo, R. Accad. d. Scienze d. Instituto di Bologna. Elected a Fellow of the Royal Society. | XXIII. XXIV. XXV. |
| Do. 2nd edition | 1893 | . . . . . . . . . . | XXVI. |

# PRECIS OF CONTRIBUTIONS TO PHYSIOLOGY

*In the following "précis" I have not attempted to give any minutely detailed list of contents, but only memoranda of such points as appear to me on reconsideration to be definite and significant. When possible, quotation is made from the short paragraphs setting them forth in my* "Introduction to Human Physiology," *or from independent reviews, on the presumption that in such instances the previous exposition to criticism has been to some extent a test of viability.*

## I. Die Spannung in den Vorhöfen des Herzens während der Reizung des Halsmarkes. *Du Bois-Reymond's Archiv*, 1878, p. 525.

Work done at Leipzig, forming part of the investigation of vascular and cardiac nerves, carried out by various observers under the guidance of Professor Ludwig.

*Chief results and conclusions.*—Tetanisation of the spinal cord causes a distension and arrest of the left auricle; this is a mechanical effect of increased pressure, by vaso-constriction, not a nerve-inhibition, for it can be produced by mechanical constriction of the aorta. It is not due to regurgitation from the left ventricle, for ventricular pressure may be 10 cm. Hg, while auricular pressure is *in maximo* 2 to 3 cm. No such effect is produced in the right auricle, *i.e.* there is no vaso-constriction in the lung comparable with the systemic vaso-constriction produced by tetanisation of the cord. Reasons given why medullary excitation need not be expected to produce pulmonary vaso-constriction.

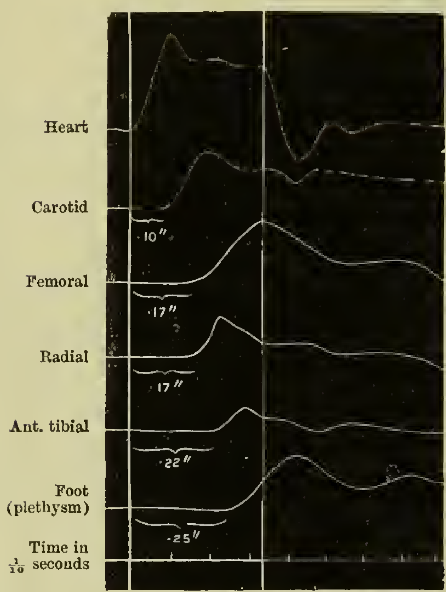
Cf. Openchowsky, "Ueber die Druckverhältnisse im kleinen Kreislaufe," xxvii. p. 233. 1882.

## II. Note of Observations on the Rate of Propagation of the Arterial Pulse-wave. *Journal of Physiology*, Vol. iii. p. 37. 1880.

Measurements by the graphic method made at Professor Burdon-Sanderson's suggestion.

The average results are shortly summarised in the following figure (not in original paper).

The Pulse-wave in the Arterial System.




| | | |
|---|---|---|
| Heart-carotid interval | | 10 |
| Heart-radial | „ | 17 |
| Heart-femoral | „ | 17 |
| Heart-tibial | „ | 22 |
| Carotid-radial | „ | 7 |
| Femoral-tibial | „ | 5 |

## III. Recurrent Pulsation in the Radial Artery. *Practitioner*, 1880, p. 412.

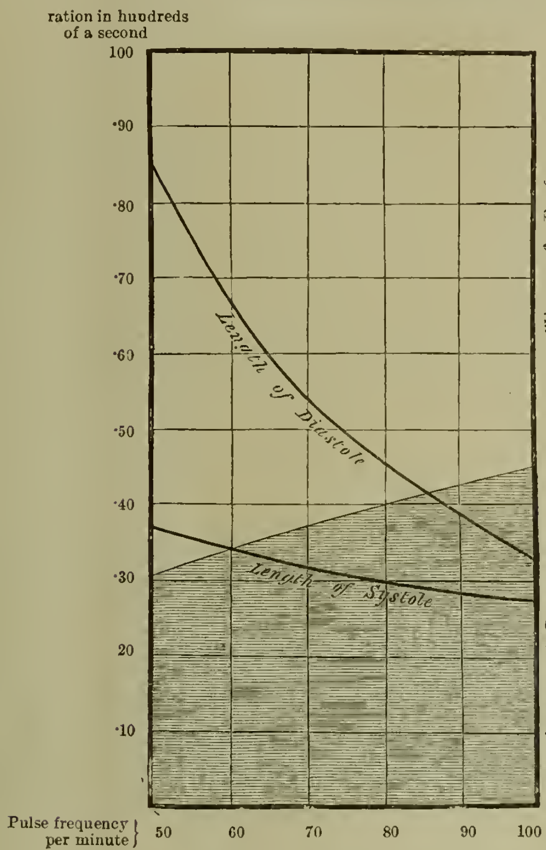
On account of free palmar anastomosis it is necessary to compress the ulnar as well as the radial artery in feeling the pulse for tension. A more or less marked "recurrent" pulse felt in the radial artery below a point of compression indicates a more or less relaxed state of the peripheral arterioles.

Note.—At the time of publication, no previous observations of this point were known to me. It is, however, alluded to in Jaccoud's "Clinique Médicale." The term "recurrent pulse" and the precaution to be observed are now matters of common knowledge. (Cf. Ringer's "Therapeutics," 9th edition, 1882, p. 18.) The fact itself, as well as the method of feeling the pulse there recommended, is described at length in Ewart's "How to Feel the Pulse," London, 1892, pp. 70, 71, 75.

## IV. Sur la Durée de la Systole Cardiaque. *Progrès Médical*, 1882, May 6.

The duration of systole varies with varying frequency of the heart's beat. From measurements obtained by the graphic method, the following averages were obtained. These points are exhibited in the accompanying figure and table.

Duration of Systole and of Diastole with Different Pulse-frequencies.




Pulse-frequencies per minute are indicated along the abscissa. Durations of systole and of diastole are given in hundredths of a second. Their respective curves show that the systole shortens by about $\frac{2}{100}$ second for each increase of 10 beats per minute, and that the diastole shortens by about $\frac{10}{100}$ second.

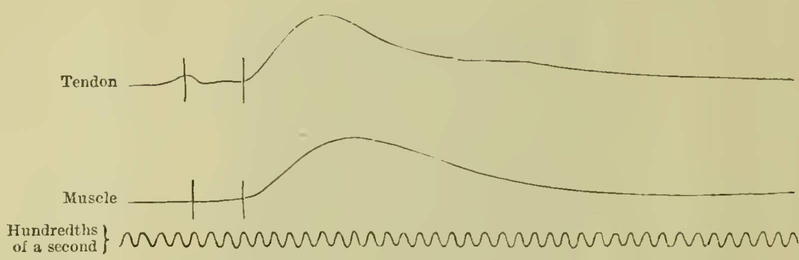
The shaded and unshaded portions represent respective time of work and time of rest at various pulse-frequencies.

| Pulse-frequency per minute | Duration of systole in hundredths of a second | Duration of diastole in hundredths of a second | Ratio of systole to cardiac cycle | Hours of work per diem |
|---|---|---|---|---|
| 50 | 37 | 83 | ·31 | 7·5 |
| 60 | 34 | 66 | ·34 | 8·2 |
| 70 | 32 | 54 | ·37 | 8·9 |
| 80 | 30 | 45 | ·40 | 9·6 |
| 90 | 28 | 38 | ·42 | 10·2 |
| 100 | 27 | 33 | ·45 | 10·8 |

## V. On Muscular Spasms known as Tendon-Reflex. *Brain*, 1880, p. 179.

Evidence by time-measurements that the phenomenon is not (as was then generally believed) a reflex action, but a direct muscular response of which a necessary condition

is the reflex tonus of the spinal cord. (Cf. also "Lancet," 1881, vol. ii. p. 83.) The average rhythm of tremor and clonus is 8 to 10 per second.



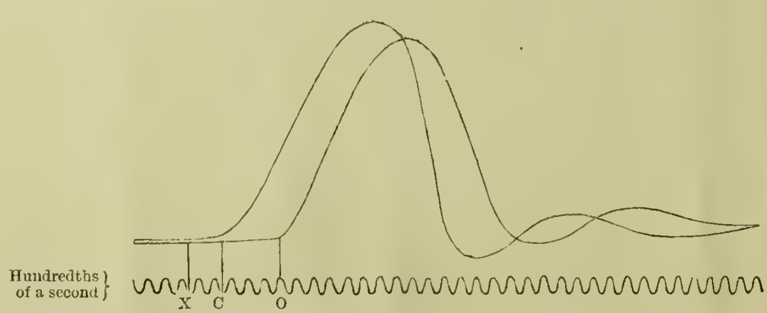

Comparison between the stimulus-to-contraction intervals observed, with percussion of the Ligamentum Patellæ (Tendon) and with direct electrical excitation of the Rectus Femoris (Muscle). Man.

## VI. Nouvelles Expériences sur les Phénomènes nommés Réflexes Tendineux (with Dr. J. L. Prévost). *Revue Médicale de la Suisse Romande*, 1881.

Four experiments on rabbits made conjointly with Dr. Prévost to test the objection that *crossed* reflex proves the phenomenon not to be a direct response. Percussion of the knee of a limb of which all nerves are cut causes contraction of the opposite limb, *i.e.* direct excitation of the opposite limb by vibrations transmitted along the bones.

## VII. Sur le Temps perdu de la Contraction d'ouverture. *Archives de Physiologie*, 1882, p. 383.

The anodic break contraction (upon man) has a latent period 0·04 longer than that of the kathodic make contraction. An anelectrotonic depression of excitability may last for 0·05 second after cessation of the polarising current.




Comparison between the stimulus-to-contraction intervals by closure (c) and by opening (o) of a galvanic current. Median nerve. Flexors of the fingers.

VIII. On the Influence of the Galvanic Current on the Excitability of the Motor Nerves of Man (with Dr. de Watteville). *Philosophical Transactions of the Royal Society*, 1882, p. 961.

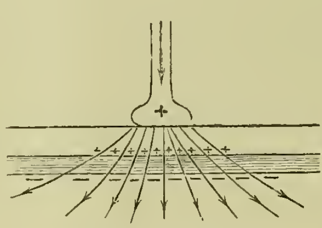
The main outcome of these observations may be most briefly indicated by quoting two passages from " An Introduction to Human Physiology," 1st edition, 1891.[1]

" *The formula of contraction on man.*—The above statements are based upon experiments with the nerves of frogs; experiments on man give results of which the principle is the same, but with differences which are owing to differences in the conditions of experiment. In the case of a frog's nerve cut out of the body, the points of entrance and of exit of the exciting current are usually chosen some distance apart, so that the kathode and anode are distinct, the current entering the nerve at one electrode and leaving it at the other. In the case of human nerve the conditions are different, for the nerve is imbedded in the tissues below the skin. A pair of electrodes cannot be applied to a nerve so as to send a current in at one point, out at another point; so that it is incorrect to speak of 'ascending' and 'descending' currents under such circumstances, and it is useless to attempt to study the effects when both electrodes are applied along the course of one and the same nerve. We must apply one electrode only to the nerve, and attend to its effects alone, completing the circuit through a second electrode which is applied according to convenience to some other part of the body. Confining our attention to the first electrode, let us see what will happen according as it is *anode* or *kathode* of a galvanic current. If this electrode be the anode of a current, the latter enters the nerve by a series of points, and leaves it by a second series of points; the former or proximal series of points collectively constitutes the *polar* zone or region, the latter or distal series of points collectively constitutes the *peripolar* zone or region. In such case the polar region is the seat of entrance of current into the nerve, *i.e.* is *anodic*; the peripolar region is the seat of exit of current from the nerve, *i.e.* is *kathodic*. If on the contrary the electrode under observation be the kathode of a current, the latter enters the nerve by a series of points which collectively constitute a 'peripolar' region, and it leaves the nerve by a series of points which collectively constitute a 'polar' region. The current at its entrance into the body diffuses widely, and at its exit it concentrates; its 'density' is greatest close to the electrode, and the greater the distance of any point from the electrode, the less the current density at that point; hence it is obvious that the current density is greater in the polar than in the peripolar region.

"These conditions having been recognised, we may apply to them the principles learned by study of frogs' nerve under simpler conditions. Seeing that with either pole

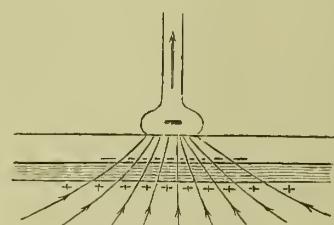
[1] The principle here stated was derived from a suggestion made by Helmholtz at the Nat. Med. Verein, Heidelberg, 1867.

of the battery, whether anode or kathode, the nerve has in each case points of entrance (constituting a collective anode), and points of exit to the current (constituting a collective kathode), and admitting as proved that make excitation is kathodic, break excitation anodic, we may with a sufficiently strong current expect to obtain a contraction at make and at break with either anode or kathode applied to the nerve. And we do so in fact. When the kathode is applied, and the current is made and broken, we obtain a *kathodic make contraction* and a *kathodic break contraction*; when the anode is applied, and the current is made and broken, we obtain an *anodic make contraction*



Anode of Battery.

Polar region of nerve is anodic.
Peripolar region of nerve is kathodic.



Kathode of Battery.

Polar region of nerve is kathodic.
Peripolar region of nerve is anodic.

and an *anodic break contraction.* These four contractions are, however, of very different strengths; the kathodic make contraction is by far the strongest; the kathodic break contraction is by far the weakest; the kathodic make contraction is stronger than the anodic make contraction; the anodic break contraction is stronger than the kathodic break contraction. Or otherwise regarded, if, instead of comparing the contractions obtained with a 'sufficiently strong' current, we observe the order of their appearance with currents gradually increased from weak to strong, we shall find that the kathodic make contraction appears first, that the kathodic break contraction appears last, and the formula of contraction for man reads as follows:—

| | | | | |
|---|---|---|---|---|
| Weak current . . . . . | K.C.C. | — | — | — |
| Medium current . . . . . | K.C.C. | A.C.C. | A.O.C. | — |
| Strong current . . . . . | K.C.C. | A.C.C. | A.O.C. | K.O.C. |

"That such should be the normal order of appearance is fully accounted for by the following considerations:—

| In the | The nature of the stimulus is | The situation of stimulus is | Conditions of excitation |
|---|---|---|---|
| K.C.C. | Kathodic | Polar | = best stimulus in best region |
| A.C.C. | Kathodic | Peripolar | = best stimulus in worst region |
| A.O.C. | Anodic | Polar | = worst stimulus in best region |
| K.O.C. | Anodic | Peripolar | = worst stimulus in worst region |

which also account for an apparent anomaly, viz. that sometimes the anodic closure contraction precedes the anodic opening contraction, while sometimes this order is reversed;

this difference depends upon relative current densities in the two regions, which are determined by the nature of the tissues by which the nerve is surrounded. In testing this point we shall hardly fail to notice a very evident token of the fact that polar and peripolar excitation is differently localised in the nerve; the muscles that contract to anodic make are not the same as those that contract to anodic break, if, *e.g.*, the exploring electrode is applied to the median nerve. This point need not, however, be further discussed here.

"The latent period of the break contraction on man is exceedingly and constantly long (·05″); on the frog its duration is very variable, sometimes very short, sometimes very long. With strong currents, it is usual on man to obtain tonic contraction during the passage of the current—*galvanotonus*—as well as single twitches at make and at break.

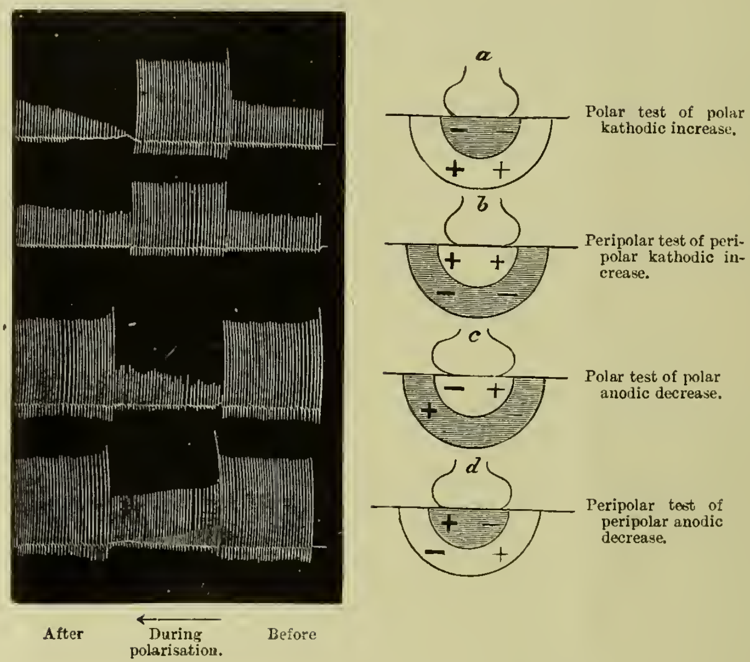
. . . . . . . . . .

"*Experiments on man.*—The above conclusions are based upon experiments made upon frogs' nerves. Experiments on man give similar results with minor differences, owing to differences in the conditions of experiments. As regards frogs' nerve, it is isolated, and the test is applied separately from the polarising current, induction currents being most convenient for testing the extrapolar region, while mechanical stimuli are best adapted for testing the intrapolar region. As regards human nerve imbedded in the tissues, such a mode of testing is not possible, and it is necessary to adopt some means for insuring that the test shall coincide with the polarised region of the nerve. This can be effected by conjoining in one circuit the testing with the polarising current, or in the case of mechanical stimuli by applying the latter through the electrode of the polarising current.

"The effect of an induction shock alone is compared with its effect in the presence of a polarising current; the difference observed is owing to the modification of excitability which the polarising current produces. The polar effects under the conditions of application of electricity to the human body, and the distinction between polar and peripolar excitation (p. 364), must be borne in mind in this connection. Remembering that a current entering or leaving the body through an electrode applied over a nerve has in that nerve a polar and a peripolar region—polar of the same sign as the electrode, peripolar of the opposite sign; remembering further that make excitation is kathodic, break excitation anodic, it is easy to understand the effects of various possible combinations between testing and polarising currents. If the induction current is used as the test, the combinations which it is possible to form at the exploratory electrode with a polarising current in the same circuit are as follows:—

1. Kathode of testing current, and of polarising current.
2. Anode of testing current, and of polarising current.
3. Kathode of testing current, and anode of polarising current.
4. Anode of testing current, and kathode of polarising current.

"Putting these four cases to the test, it will be found that excitability is *increased* in the polar region when it is *kathodic*, *diminished* when it is *anodic*, and that similarly, but in smaller degree, excitability is increased in a peripolar kathodic region, diminished in a peripolar anodic region.




"Similar results follow the application of other tests—make and break of a constant current, alone, and in the presence of a polarising current in the same circuit—mechanical stimulation alone and during the passage of a polarising current—viz. increased excitability in a kathodic region, diminished excitability in an anodic region."

IX. On the Influence of the Galvanic Current on the Excitability of the Sensory Nerves of Man (with Dr. de Watteville). *Proceedings of the Royal Society*, 1882, p. 366.

A verification on *sensory* nerves of the phenomena described in the previous paper relating to motor nerves. Experiments of this nature on man, as compared with analogous experiments on animals, present the advantage that alterations of sensory excitation can be better appreciated by the subjective evidence of sensibility than by the objective signs from which inferences are drawn.

X. Experiments and Observations relating to the process of Fatigue and Recovery. *First Report, British Medical Journal*, July 1885. *Second Report, British Medical Journal*, July 1886.

The general tenor of these two papers will be most briefly presented by quotation of the following account in the *British Medical Journal*, to which may be added the remarks (1) that the first report contains a description of a new application of photography to the recording of galvanometric deflections, (2) that the second report was a brief preliminary communication of facts more fully set forth in No. XI.

## THE PROCESS OF FATIGUE AND RECOVERY.

"The conclusions reached by Dr. Waller concerning the part played by the motor end-plates in the process of fatigue, and in the allied process of degeneration, are of special interest and importance, and justify our acceptance of the generalisation that the junction of nerve and muscle is a weak link in the chain, and is the first to suffer in its transmitting-function by poison, by excessive action, and by disorderly nutrition. We have, in short, under these last two conditions, an effect precisely similar to that which is brought about by the action of curare; and we see that an identical result—namely, the establishment of a block between nerve and muscle—can be produced by curare, by fatigue, and by degeneration; that is to say, by agents in the toxicological, in the physiological, and in the pathological domains: a generalisation which is still further extended to include the changes which naturally occur at death. Dr. Waller's experiments on this last point are not advanced as being entirely conclusive. The problem here is to examine whether, in the dying organism, the excitability of nerve outlasts the excitability of muscle by stimuli applied to its nerve; and the only method by which this could be accomplished was by the observation of the 'negative variation' as the index of excitation occurring in the nerve when it had ceased to have action on muscle. This method was followed, and instruments were devised for the purpose of recording the results. A complication, however, arises, owing to the development of electrotonic currents which might mask or be mistaken for the negative variation; and Dr. Waller promises to repeat these experiments with additional precautions. These experiments, relating to the motor end-plate, also go far to prove that it is an organ that can be fatigued; and, therefore, when called into action, a force-producing organ, and not merely a passive conductor, like nerve, as was held by Tschiriew. The last-named observer stated that fatigue by excitation of nerve runs a parallel course with fatigue by direct excitation. The present report contains, however, curves (fig. 19), in which the fatigue-decline is more rapid for indirect than for direct excitation.

"Another question of practical importance which is broached in these experiments is that of the principal site of fatigue, when normal voluntary action is sustained or

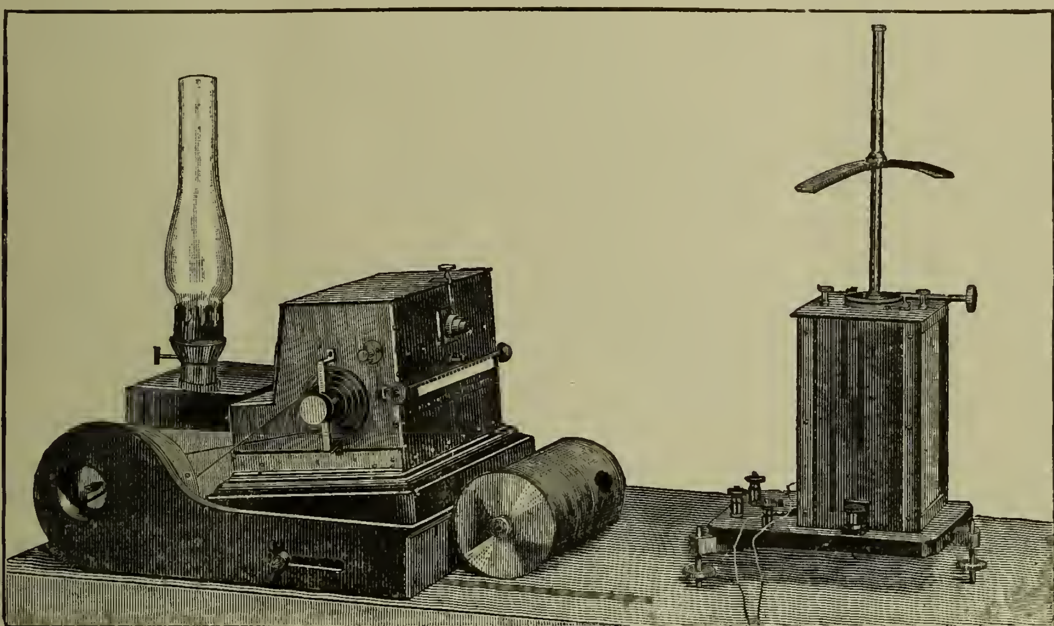
repeated for long periods. It clearly results, from the experiments made by Dr. Waller on this point, that, when central nerve-cell, nerve-fibre, and muscle are together called into play in the accomplishment of repeated voluntary efforts, it is the central cell that is the weakest link in the chain ; and that voluntary action grows weaker as fatigue increases—not because either muscle or nerve are becoming exhausted, but because the central motor is expending its power. Dynamometric observations show diminished voluntary power at a time when the excitation of nerve or muscle gives none of the ordinary signs of fatigue at the periphery ; evidence of peripheral fatigue appears, indeed, to be obtainable with a difficulty which contrasts strongly with the ease and rapidity of the occurrence of voluntary fatigue. The bearing of these observations upon some of our guiding notions in medical practice is obvious, and appears at first sight to be out of harmony with the recent experiments of Zabludowski and others, and the undoubtedly good effects of 'massage,' which can only be understood on the supposition that fatigue is, in part, peripheral. This is, however, not excluded by the above observations ; an instance of peripheral fatigue by excessive central action is given in the case of strychnia acting on the spinal cord ; and the conclusion appears to be that the process of fatigue expresses itself at both ends of the nerve—more, however, at its central than at its peripheral end. Data are still wanting, however, before we may assign to each constituent of the nervous arc its share in the depression of function that results from expended activity. We know already, from the older experiments of Du Bois-Reymond, and the more recent experiments of Wedenski and of Bowditch, that the nerve proper has little or no share in the depression ; that it does not expend force, but is merely a passive conductor ; that it is, therefore, practically unsusceptible of fatigue. Bernstein's older experiments, on the course of fatigue and recovery in nerve, have been entirely supplanted by these modern experiments ; and we now require a comparison of the process in the nerve-centre with that at the periphery, and not the comparison of muscle with nerve in this respect, seeing that the last-named organ is practically independent of functional fatigue and recovery.

"Dr. Waller's report contains further an account of experiments showing that the effect of a poison, when it has added itself to the normal effect of which an organ is capable in response to excitation, can itself be dissipated in consequence of a series of excitations, and reaccumulated during an interval of repose, even if the organ be completely isolated from any fresh supply of the poison. Such phenomena are shown to occur in the case of the action of veratria upon muscle, and in that of strychnia upon the spinal cord ; the veratria character disappears from muscle in consequence of repeated action, and returns during subsequent repose ; the strychnia character disappears from the spinal cord in consequence of repeated action, and returns during repose. The analogy of these phenomena with each other and with the normal process of fatigue and recovery is complete ; they differ only in the rapidity with which they are developed. The process in the cord is evidently of the same causation as the changes in excitability recently observed by Walton upon animals poisoned by strychnia, to the

effect that the cord, after repeated excitation, regains its property of summating stimuli, and loses this property during subsequent repose.

" The course of an intoxication has many points of resemblance with the course of fatigue; both are usually characterised by an initial increase, and subsequent decline of excitability; but the case of the action of strychnia upon the cord appears to be exceptional; the excitability is increased, even in advanced intoxication, in the presence of signs of muscular exhaustion. Under such conditions, however, a sign of fatigue is present in the form of the well-known delay of reflex action, which increases as the toxic effects deepen, and is an index of a gradually increasing block of transmission in the cord. Dr. Waller reports experiments made in order to test the point of the nervous

Galvanograph.



ar c at which this block of transmission occurs, and has found that it does so at first exclusively, and later chiefly, at the junction of the afferent nerve with the spinal cord, for at first the time of reaction is prolonged in the absence of any retardation in the transmission of nervous impulses within the cord; and later, when such retardation does take place, it is small in comparison with the prolongation of the time of reaction.

" The report concludes with some important observations upon the alteration of resistance which is caused in the human body during the passage of the galvanic current. But it is not our intention, nor have we attempted, to summarise the entire report, which is itself a concise summary of observations, and a preface to further study of an important borderland province between physiology and pathology."

Cf. Mosso, " Die Gesetze der Ermüdung," Du Bois-Reymond's " Archiv," 1890, p. 89.

## XI. On the Action of the Excised Mammalian Heart (with Professor E. Waymouth Reid). *Philosophical Transactions of the Royal Society*, 1887, p. 215.

The purport of this paper is given in an abstract sent to the Académie des Sciences.[1]

It was reported upon by the " Commission d'examen " (MM. Marey, Charcot, Lappey, Ranvier, and Brown-Séquard) in the following terms :[2]

"Ce travail contient nombre de faits nouveaux et très intéressants à l'égard des phénomènes électriques du cœur, de la durée de l'action rhythmique des quatre parties de cet organe après l'excision, et de la lenteur que peut acquérir l'onde de contraction cardiaque dans certaines circonstances. Nous pourrions nous borner, pour légitimer notre conclusion à l'égard de la récompense que nous proposons d'accorder à ces physiologistes, à renvoyer à l'analyse qu'ils ont publiée de leur Mémoire dans les Comptes rendus (séance du 31 Mai dernier, p. 1547). Mais nous croyons devoir rappeler quelques-uns des points établis par ces auteurs.

"Ils ont fait voir que le cœur excisé des mammifères se comporte comme celui des batraciens, quant au passage de l'onde de contraction, mais avec quelques différences. Dans le cœur des mammifères, la variation n'est pas toujours diphasique. Elle ne l'est pas aussitôt après l'excision, mais le devient plus tard, d'ordinaire après quelques minutes. Les mouvements du galvanomètre et de l'électromètre indiquent, dans les variations monophasiques, une négativité prédominant soit à la pointe, soit à la base ; dans la variation diphasique, une négativité à la pointe, puis à la base, ou vice versa. Une autre différence á été trouvée entre le cœur des mammifères et celui de la grenouille ; c'est que le mouvement de la pointe s'est montré presque toujours avant celui de la base, tandis que chez la grenouille c'est toujours l'inverse qui a lieu.

"Les expériences de ce physiologistes ont été excessivement multipliées et leur Mémoire donne un nombre très considérable de graphiques établissant l'exactitude de leurs conclusions.

"La commission propose de donner aux auteurs de ces intéressantes recherches une mention honorable."

## XII. Note sur la force électromotrice d'un animal à sang chaud (chat) après la mort. *Archives de Physiologie*, 1888, p. 457.

Observations of the great length of time after death during which the electromotive action persists in the muscles of warm-blooded animals.

[1] *Comptes Rendus de l'Académie des Sciences*, 1887, p. 1547. [2] *Ibid.* 26 Décembre 1887, p. 1370.

XIII. A Demonstration on Man of Electromotive Changes accompanying the Heart's Beat. *Journal of Physiology*, 1887, p. 229.

XIV. On the Electromotive Changes connected with the Beat of the Mammalian Heart and of the Human Heart in particular. *Philosophical Transactions of the Royal Society*, 1889, p. 169.

XV. Détermination de l'action électromotrice du cœur de l'homme.[1] *Archives de Physiologie*, 1890, p. 146.

The above three papers, of which the first contains the description of a " demonstration " and the third a summary account of a more complete " determination," contain a series of studies relating to the electrical action of the human heart.

The main facts may be briefly presented by the following figures and descriptions in " An Introduction to Human Physiology," 2nd edition, pp. 391–2.

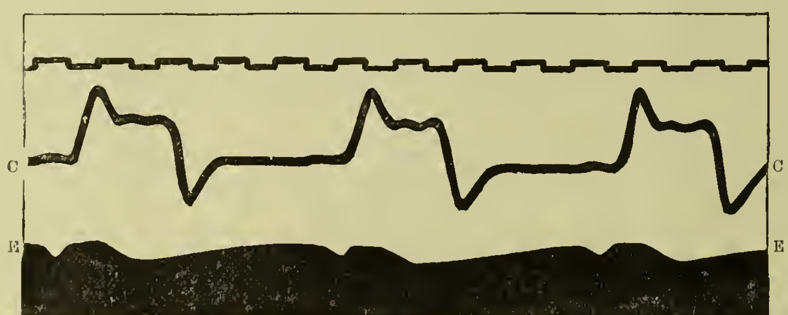

[1] *Prix Montyon de Physiologie expérimentale*, 1888. *Premio Aldini sul Galvanismo*, Bologna, 1892

"Let A and B respectively represent apex and base of the ventricular mass. Then, if at any moment a difference of potential should arise between A and B, a current *c c c* will be established along and around the axis A B. The line O O will represent the plane of zero potential or equator. The lines *a a a*, *b b b* will represent equipotential curves around A and B. A difference of potential between A and B will be manifested if the two leading off electrodes are applied on opposite sides of the equator O O; no such difference will be manifested if both electrodes are on the same side of the equator. The equator O O will divide the body into two asymmetrical parts, (1) a portion *b b b* including the head and right upper extremity, (2) a portion *a a a* including the three other extremities.

"If we 'lead off' to the electrometer by any two points *a* and *b*, on opposite sides of the equator (*e.g.* by the mouth and the left hand), we shall see the mercury pulsate with each beat of the heart. If we lead off to the electrometer by any two points *a* and *a*, or *b* and *b*, on the same side of the equator (*e.g.* by the mouth and the right hand), no such pulsation of the mercury will be visible."

Cf. Bayliss and Starling, "Internat. Monatschr. f. Anat. u. Physiol." 1892.

Human Heart. Electrical Variation, E E; and Simultaneous Cardiogram, C C.




The leads off to the capillary electrometer were from the mouth to the sulphuric acid, and from the left foot to the mercury.

The MS. of Paper No. XIV. was presented to the Académie des Sciences, Paris, and adjudicated upon in the following terms:[1]

## PRIX MONTYON (PHYSIOLOGIE)

(Commissaires: MM. Marey, Ranvier, Bouchard, Charcot, Duchartre, Bornet; Brown-Séquard, rapporteur).

"Le Dr. Augustus D. Waller a présenté à l'Académie, pour le prix de Physiologie expérimentale, un travail extrêmement remarquable sur la détermination électromotrice

[1] *Comptes Rendus de l'Académie des Sciences*, 24 Décembre 1888.

du cœur de l'homme. Il a découvert que des états électriques variés se succèdent dans le cœur des mammifères et celui de l'homme pendant la systole et le repos de cet organe, et que des états électriques analogues se montrent aussi successivement dans les diverses parties du corps. Pendant la diastole et le repos du cœur, cet organe et le corps entier ne montrent aucune variation électrique, négative ou positive. Lorsque la systole cardiaque a lieu, la contraction commençant à la pointe du cœur, on y trouve une variation négative, tandis qu'il y a à la base des ventricules une variation positive. Simultanément, on voit apparaître une variation négative dans le membre inférieur droit, dans les deux membres gauches, dans le tronc, depuis sa partie inférieure jusqu'aux côtes à droite et jusqu'à l'épaule à gauche, tandis qu'une variation positive se montre dans le reste du corps (tête et cou, bras droit et un peu plus que la moitié droite du thorax).

"L'inverse a lieu dans le cœur et le corps entier quand la contraction systolique a gagné la moitié supérieure des ventricules. Les parties négatives deviennent alors positives, et vice versa. Quand la diastole arrive, l'équilibre électrique se rétablit partout (cœur et corps) jusqu'à ce qu'une nouvelle systole commence.

"Lorsqu'on examine l'état électrique des mains d'un homme plongées dans un liquide, l'une dans un vase, l'autre dans un autre, on constate successivement et à chaque période cardiaque : d'abord de la négativité à la main gauche et de la positivité à la main droite ; ensuite l'inverse ; enfin la neutralité électrique. Ces trois états correspondent, le premier au commencement, le second à la fin de la systole ventriculaire, et le troisième à la diastole et à la pause du cœur. Ou peut ainsi, à l'aide des changements électriques, non seulement compter les mouvements du cœur, mais encore les mesurer quant à leur durée.

"L'auteur a eu la chance de recontrer un homme ayant une transposition des viscères, et chez lequel la pointe du cœur est à droite. Dans ce cas les choses étaient changées en harmonie avec les faits et les idées du Dr. Waller. Le bras droit était négatif au début de la systole cardiaque, alors que le bras gauche était positif.

"Chez les mammifères, comme le chat, ayant un cœur sans déviation de la pointe à gauche ou à droite, les deux membres antérieures et la moitié supérieure du thorax, ainsi que la tête et le cou, sont à l'état positif, alors que le reste du corps et les membres abdominaux sont à l'état négatif au début de la systole.

"En mettant les deux membres antérieurs d'un chat dans un vase contenant un liquide et les deux postérieurs dans un autre vase, on peut compter et mesurer les mouvements du cœur de l'animal par les changements électriques.

"Ce sont là des faits du plus haut intérêt, et qui conduiront probablement à des résultats d'une grande importance lorsque M. Augustus Waller aura trouvé leur explication."

Here follows the account of Professor Fredericq's work. . . . .

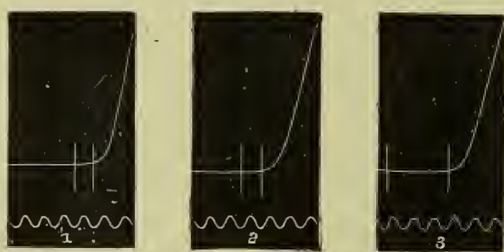
"En présence de travaux aussi originaux, aussi remarquables que ceux de M. Augustus D. Waller et de M. Léon Fredericq, la commission croit devoir proposer à

l'Académie de partager entre ces deux ingénieux expérimentateurs le prix de Physiologie expérimentale."

Paper No. XV. was presented to the R. Accademia delle Scienze dell' Instituto di Bologna, and on its account the "Premio Aldini sul Galvanismo (Elettricità Animale)" was awarded to the author (1892).

XVI. On the Physiological Mechanism of the Phenomenon termed Tendon-Reflex. *Journal of Physiology*, 1890, p. 383.

Repetition on the rabbit of time-measurements previously made on man, with conclusions similar to those stated in Paper V.




Time-measurements of (1) a direct contraction, (2) of the tendon phenomenon, (3) of a reflex contraction (on the rabbit).

XVII. A new Colour-contrast Experiment (*Proceedings of the Physiological Society*). *Journal of Physiology*, 1891.

Modification of Meyer's colour-contrast experiment. Argument that the modified experiment is more consonant with the psychological theory of Helmholtz than with the physiological theory of Hering.

XVIII. A possible Use of the Membrana Tectoria (*Proceedings of the Physiological Society*). *Journal of Physiology*, 1891.

Exposition of a theory to the effect that auditory stimulation may be produced by "pressure-patterns" of the hair-cells against the membrana tectoria.

XIX. AN INTRODUCTION TO HUMAN PHYSIOLOGY. (Longmans & Co.)

1st edition (pp. 612, with 292 illustrations), 1891.
2nd edition (pp. 632, with 305 illustrations), 1893.

Notices and critical reviews in: "British Medical Journal," January 2, 1892; "Lancet," January 30, 1892; "Nature," February 11, 1892; "Brain," July 1892, and other journals.

Papers XX. (on the sense of effort) and XXV. (on the functional attributes of the cerebral cortex) deal with matters of mainly psychological interest, from a physiological standpoint. The nature of the arguments, which of necessity deal with much sub-positive matter, renders it difficult to give a short abstract of their contents. Experimental points presenting themselves in connection with psychological considerations involved in these two papers, and susceptible of actual demonstration, are dealt with in papers XXI., XXII., XXIII., and XXIV.

## XX. The Sense of Effort: an Objective Study. *Brain*, 1891, pp. 179–249.

The main argument in this paper has been summarised as follows in "An Introduction to Human Physiology" (2nd ed., p. 550).

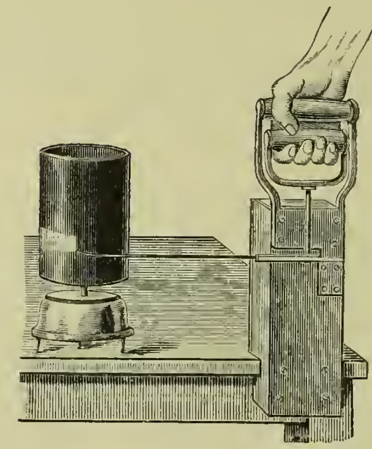
"Muscular sense, sense of movement, sense of effort, are terms used to denote the sensation that accompanies all voluntary muscular contractions. The factors of this composite sensation are:—(1) *peripheral*, arising from variations of tension and of pressure in the moved organs, *i.e.* in tendons, ligaments, cartilages, possibly in the muscle itself, certainly in the skin of the part; (2) *central*, arising from material changes accompanying the elaboration and emission of motor impulses.

"Whether a central as well as a peripheral factor contributes to the sensation of movement or effort has been much debated, and is still denied by some authorities, who regard it as of exclusively peripheral origin. The view that the central state is implicated in the formation of the sensation is materially supported by the objective signs of fatigue. Admitting that material changes *after action* occur in the same parts as material changes *with action*, we may learn the incidence of the effect by studying the incidence of the after-effect. Now the after-effect of muscular action, subjectively felt as fatigue, is demonstrable by objective signs at the centre as well as at the periphery; from which we infer that the motor effect, which is subjectively felt as the sensation of movement or of effort, is associated with material changes at the centre as well as at the periphery. This is to say, that the sensation called 'muscular sense,' 'sense of movement,' 'sense of effort,' is associated with changes *at the centre and at the periphery*; we have no right to say that it is caused by changes in either of these situations to the exclusion of the other."

The same paper contains a description of the "Dynamograph," employed in the observations described in Paper XX. for the study of voluntary and of electrically excited fatigue.

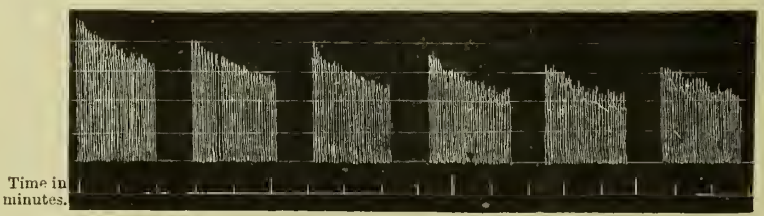
"The value of the dynamometer is much increased if it is converted into a *dynamograph*; the manner of maintenance of a prolonged maximum effort for regular periods, or the character of a series of maximum efforts for regular periods, may then be recorded on a slowly travelling surface, *e.g.* a cylinder on the hour axis of an ordinary

Dynamograph.

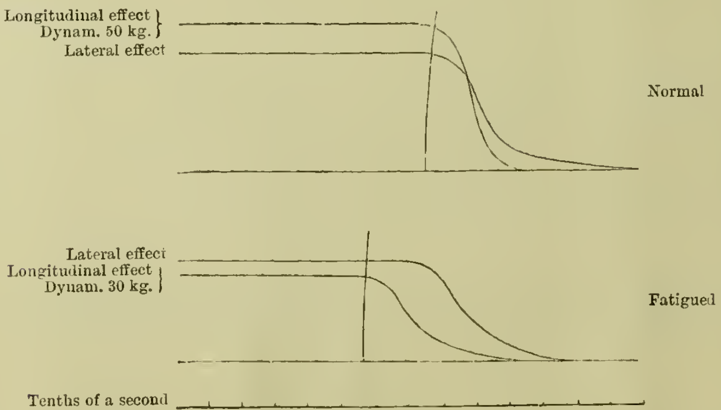


clock; and from such records an estimate may be formed of the muscular strength, of its rate of decline in a succession of efforts, and of its rate of recovery from such decline.[1]"

Dynamograph Tracing.




XXI. A peculiar Fatigue-effect on Human Muscle (*Proceedings of the Physiological Society*). *Journal of Physiology*, 1891, p. lv.




Simultaneous tracings of the longitudinal or dynamic effect, and of the latera or rigor effect, in the Normal and in the Fatigued states respectively, in maximal voluntary contraction of the muscles of the Forearm of Man.

[1] *Intr. H. Physiol.* p. 339.

A simultaneous record of the longitudinal and lateral effects of muscular contraction taken from the muscles of the forearm exhibits practically simultaneous beginning and end of effects in the normal state, but in the state of fatigue the lateral effect commences to cease nearly one-tenth of a second later than the longitudinal effect. The change is characteristic of voluntary fatigue and is not produced by direct electrical tetanisation.

XXII. The Muscular Sound during Galvanotonic Contraction (*Proceedings of the Physiological Society*). *Journal of Physiology*, 1891, p. 56.

Demonstration of a muscular sound during "galvanotonus" identical in pitch with that heard during voluntary tetanus.

XXIII. Experiments on Weight-discrimination (*Proceedings of the Physiological Society*, January 30, 1892

The discrimination between different weights is more delicate: (1) by voluntary than by electrically excited contraction; (2) by galvanisation than by faradisation; (3) by muscle electrically excited than by nerve electrically excited.

XXIV. On the Inhibition of Voluntary and of Electrically Excited Muscular Contraction. *Brain*, 1892, p. 35.

Experimental and critical study regarding the question of peripheral inhibition of voluntary muscle.

*Conclusions:*—(1) "Anodic inhibition" and "kathodic excitation" are normal phenomena of human, as of all animal muscle and nerve. (2) There is no proof of the passage of inhibitory impulses to voluntary muscle, either by the ordinary motor channels or by any special inhibitory fibres.

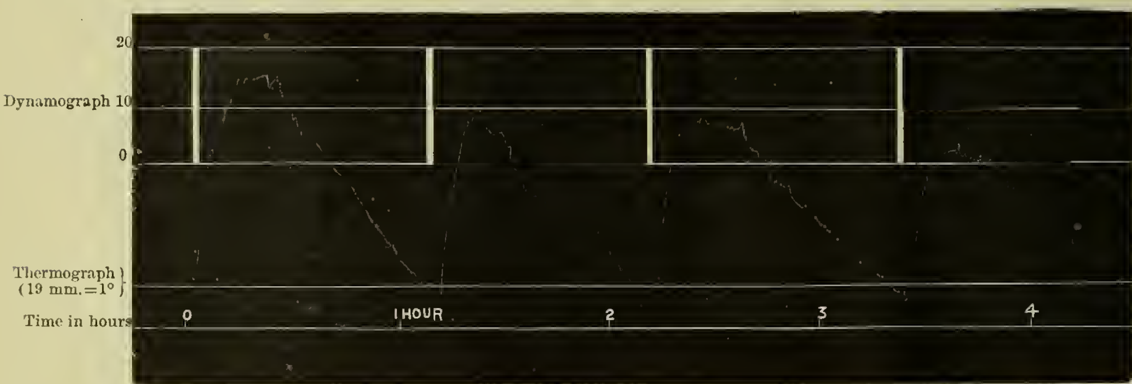
XXV. On the Functional Attributes of the Cerebral Cortex. *Brain*, 1892, pp. 329–396.

Historical and critical study of experimental data relating to the cerebral cortex, and of their psychological significance.

XXVI. Expériences myothermiques sur l'homme. *Proceedings of the Physiological Congress of Liège*, 1892.

On Calorimetry by Surface Thermometry and Hygrometry. *Proceedings of the Physiological Society*, November 1893.

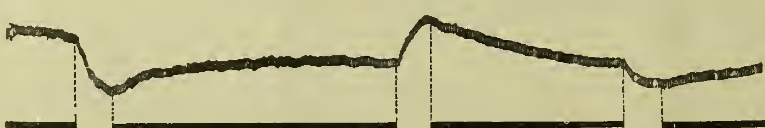
Preliminary communications embodying thermometric and hygrometric observations on man and calorimetric deductions therefrom. New methods of recording temperature variations : (1) by the galvanograph described in paper X. ; (2) by an air thermograph. Loss of heat by evaporation is separately calculated from chloride of calcium vessels weighed before and after application to the skin during a given period Local increase of surface temperature consequent upon muscular contraction—*e.g.* of a limb—is in major part due to increased blood-supply, in minor part to muscular thermogenesis. (Not yet published *in extenso.*)




| | | | | |
|---|---|---|---|---|
| Maximum rise of temperature | 1·42° | 1·27° | 1·16° | 1·05° |
| Calories calculated as emitted from the forearm and hand | 390 | 290 | 316 | 266 |

Simultaneous tracing of dynamograph (30 efforts of 20 kg., each effort lasting 2 secs. with intervals of rest of 2 secs., each series of 30 made at hour intervals) and of air-thermograph applied to the extensor muscles of the forearm. Man.

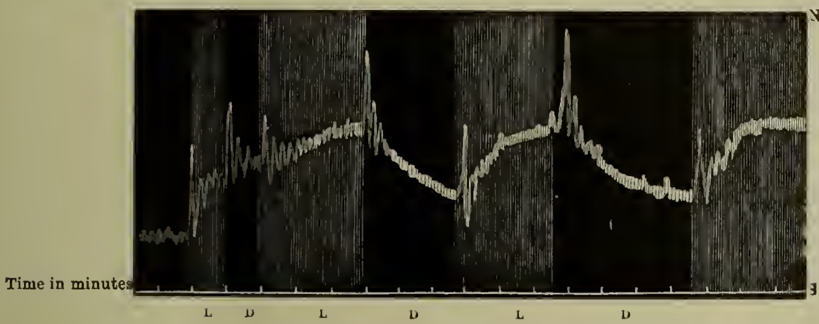
Thermo-galvanogram to exhibit the rise of temperature in isolated contracting muscle.



Two thermo-electric needles in the two gastrocnemii of a frog, and connected with a low-resistance galvanometer ; the spot of light from the mirror records the deflection of the magnet upon a cylinder covered by sensitive paper and revolving round a horizontal axis. Excitation of the sciatic on one side for 1 min. causes increased heat in one muscle and deflection of the magnet ; excitation on the opposite side gives deflection in the opposite direction. Periods of excitation indicated by breaks of the abscissa. In this instance the rise of temperature is considerably greater than that generally quoted, viz. according to Helmholtz, a rise of 0·1° with a tetanus lasting one minute ; according to Fick, a rise of 0·002° with a single contraction.

XXVII. On Retinal Currents. (Orally published communication to the Physiological Society, January 1895.)

Demonstration of galvanographic records of the electrical effects of light upon the retina, in continuation of the observations of Holmgren and others. (Experiments at present in progress.)




. Galvanogram to exhibit the electrical changes occurring in the retina at and during the incidence and removal of light. Frog's eyeball, forty-eight hours after excision. Standard candle at 2 feet. Temperature 5°. Nerve to north terminal of galvanometer; cornea to south terminal.

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